ARISTIDAE ELUDENDAE II: A RE-EVALUATION OF THE *ARISTIDA GIBBOSA* COMPLEX (POACEAE: ARISTIDEAE), INCLUDING *A. MARGINALIS*, *A. ORIZABENSIS*, AND *A. SORZOGONENSIS*

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ABSTRACT

Taxonomic relationships based on morphological variation among *Aristida gibbosa, Aristida marginalis, Aristida orizabensis,* and *Aristida sorzogonensis* were assessed by principal component analysis. Results of the PCA indicate two distinct clusters corresponding to *A. gibbosa* and *A. sorzogonensis*. The two taxa are distinguished by a number of vegetative and spikelet features. Within *A. sorzogonensis*, two taxa are recognized at the *forma* level based on pulvini development. *Aristida marginalis* was represented by a single specimen (the type) that was isolated between the *A. gibbosa* and *A. sorzogonensis* clusters. **Aristida sorzogonensis** f.**orizabensis** (E. Fourn.) Strahan & Allred is a new combination. A key to determine the species of the *Aristida gibbosa* complex, brief descriptions, and specimens examined are provided.

RESUMEN

Las relaciones taxonómicas basadas en variaciones morfológicas entre *Aristida gibbosa*, *A. marginalis*, *A. orizabensis*, y *A. sorzogonensis* se evaluaron empleando el Análisis de Componentes Principales (PCA). Los resultados de éste análisis indican que existen dos grupos distintos caracterizados por *A. gibbosa* y *A. sorzogonensis.* Las diferencias entre estas dos especies o grupos incluyen características vegetativas y también diferencias entre espiguillas. Dentro del grupo correspondiente a *A. sorzogonensis*, se reconocen dos taxa a nivel "forma" basados en el desarrollo de los pulvínulos. *Aristida marginalis* está representada por una sola colección (Typus) y se ubicó en forma aislada entre los grupos de *A. gibbosa* y *A. sorzogonensis*. ***Aristida sorzogonensis*** f. ***orizabensis*** (E. Fourn.) Strahan & Allred, es una nueva combinación. Se incluye una clave para determinar las especies del complejo *Aristida gibbosa*, descripciones breves y los especímenes examinados.

INTRODUCTION

The genus *Aristida* L. comprises some 250–350 species, nearly worldwide in distribution, growing in warmer, more arid environments (Allred 2003). Members are characterized by a panicle inflorescence, one-flowered spikelets, and relatively large glumes, usually larger than the floret. The florets are characterized by three awns, the two lateral awns absent or much reduced in some species, and a sharp pointed callus with a tuft of hair at the base. In some cases the lemma body is drawn out into an elongated beak below the divergence of the awns. The genus has its share of taxonomically difficult species complexes. Members of such groups often differ only slightly morphologically and commonly overlap in their geographic distribution (Allred 1984a, 1984b; Longhi-Wagner 1990).

The *Aristida gibbosa* complex is one such group. This New World complex is characterized by the following two features: 1) floret sulcate, the margins of the lemma slightly overlapping, and 2) callus short, 0.3–0.4 mm long, the attachment scar circular and tiny, 0.2–0.3 mm in diameter (Fig. 1). New World taxa corresponding to these features have received the following names (in chronological order):

Chaetaria gibbosa Nees (1829): In his ample description, Nees noted the regular branching of the culms, short lower sheaths exposing the gibbous nodes (whence the specific epithet), and folded or rolled leaf blades. Blade margins are not thickened, the marginal veins being no wider than those inward, and the adaxial surface is lacking pilose hairs except at the corners of the sheath. Panicles lack pulvini and are thus narrow and contracted. This is a South American species, and the name was unused in North and Central American works until Longhi-Wagner (1990) called attention to the sulcate lemma of numerous specimens

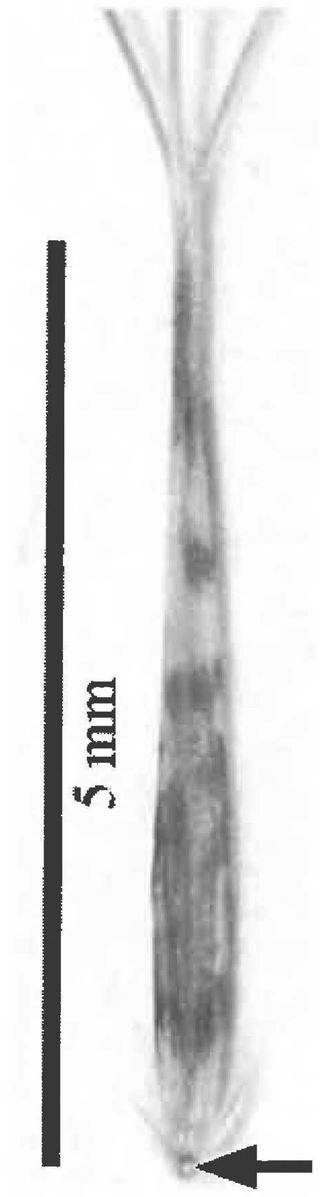


Fig. 1. Sulcate lemma with tiny circular attachment scar (arrow).

at MO and US and annotated them as this. The name was then applied, in an expanded sense, to Meso-American plants by Pohl and Davidse (1994) to include *Aristida sorzogonensis*, *A. orizabensis*, and *A. marginalis*.

Aristida sorzogonensis J. Presl (1830): Erroneously believing Haenke's specimen to be from Sorsogon on the island of Luzon in the Philippines, Presl applied the specific epithet *sorzogonensis* to his new species. It is highly probable that the specimen actually came from Central America or Mexico (annotation in 1921 on the type by E.D. Merrill; Henrard 1928). The type collection is represented by at least two sheets, both with a single flowering culm: the holotype at PR(!) has three mid- to upper blades, but lacks the base of the plant or any basal blades; an apparent isotype at PR(!) has a culm with three upper blades and two mid- to lower blades. Presl described the blades as convolute-setaceous, which the upper are, but the middle and lower blades are flat (perhaps rolled a bit upon drying) in both specimens. Blade margins are noticeably thickened, with a wide band of sclerenchyma at the margin; this is easily visible even on the upper blades that are rolled. The adaxial surface has prominent pilose hairs upwards from the throat region. A close examination of the panicle branches and pedicels reveals small (perhaps young) pulvini in nearly all the axils, with the resultant slight spreading of the axes, a feature not noted for this species in any previous works. The name *Aristida sorzogonensis* has been largely ignored or unknown by nearly all North American botanists, even though Henrard recognized it in both his Revision and Monograph of *Aristida* (Henrard 1929, 1932). Pohl and Davidse (1994) rightly called attention to the priority of *sorzogonensis* over *orizabensis* and *marginalis*, but we believe they misinterpreted the typification in tentatively applying the name *sorzogonensis* to plants with rolled, rather than flat, blades.

Aristida liebmanii E. Fourn. (1886): Fournier's description came from a collection by Liebmann (whence the specific epithet) and noted the following distinctive features: basal blades are flat and the upper blades are rolled (much as in the type of *A. sorzogonensis*), and first glumes are longer than the second. He did not call attention to the nearly complete absence of an elongated beak on the lemma, the awns immediately diverging from the apex, but this was stressed by Henrard (1927), is easily observable in the type, and was re-emphasized by Pohl and Davidse (1994). An isotype at MO(!) contains three flowering shoots and one basal portion. The margins of the blades are noticeably thickened, and the lower panicle branches are naked at the base and somewhat flexuous. Panicles are non-pulvinate. Pohl and Davidse (1994) called attention to its similarity with *A. succedeana* Henr., a species of Bolivia and Brazil that also has sulcate lemmas, flat blades, and sub-flexuous panicle branches, with the suggestion that the two may be conspecific. However, because of the scarcity of specimens further analysis and conclusions concerning this species must await the availability of more material.

Aristida orizabensis E. Fourn. (1886): Fournier's description, though short, mentions flat blades (rolled upon drying), somewhat unequal glumes, and a narrow lemma that was slightly shorter or longer than the glumes. Material came from "Valle de Orizaba," Veracruz, Mexico (whence the specific epithet), with Fournier citing two specimens, which are considered syntypes. Isosyntypes at NY(!) and US(!) have flat, curling blades with thickened margins and with long pilose hairs on the adaxial surface near the ligule, and panicles lacking pulvini. Henrard (1927) contrasted *A. orizabensis* with *A. arizonica* Vasey and *A. appressa* Vasey, two species excluded from this complex that lack sulcate lemmas.

Aristida marginalis Ekman (1911): This species was named from material collected along the dry, grassy edges of forests or woods ("in margine silvulae," whence the specific epithet) in Matto Grosso, southern Brazil. The new species is very well described by Ekman. In type material (isotypes G!, US!), sheaths are about half as long as the numerous internodes with gibbous nodes; lower blades are flat, curling, and thick-margined with pilose adaxial surfaces; the panicle is obscurely and incompletely pulvinate (i.e., with poorly developed pulvini in the axils of some branchlets and pedicels); and the lemmas are sulcate with a

short, circular callus. Longhi-Wagner (1990) subsumed this name under *A. gibbosa*, using comparisons of spikelet features such as beak length and relative glume length. The name *A. marginalis* has been applied to numerous Mexican specimens with flat, curling blades and well-developed pulvini.

This study investigates the relationships among *Aristida gibbosa*, *A. sorzogonensis*, *A. orizabensis*, and *A. marginalis* using multivariate analysis of morphological characters scored from herbarium specimens to assess species boundaries and determine the usefulness of certain traits used to distinguish them.

MATERIALS AND METHODS

For analysis of taxonomic relationships, specimens identified as *Aristida gibbosa*, *A. sorzogonensis*, *A. orizabensis*, and *A. marginalis* were obtained from the following herbaria: F, G, MO, NMCR, US, and WIS. All specimens were examined for a sulcate lemma to distinguish them as members of the *A. gibbosa* complex. A complete examination of all specimens yielded 90 OTUs (operational taxonomic units) for the analysis, including type specimens of *A. gibbosa*, *A. sorzogonensis*, *A. orizabensis*, and *A. marginalis*. The specimens used represented the full geographic distribution of the species complex from northern Mexico through Central and South America. A complete data set is available upon request. Roughly two-thirds of the specimens received that were identified in herbaria as *A. orizabensis* were actually *A. appressa*, and not included in this study. In addition to not having a sulcate lemma, *A. appressa* develops a thicker beak (0.2–0.3 mm), usually longer lemma (7–16 mm), and longer callus (0.6–1 mm) with a longer, elongated (rather than circular) attachment scar.

Each OTU was scored for 13 characters, seven discrete and six continuous (Table 1). All discrete characters were recorded for mature vegetative features as present or absent, with and without the aid of a dissecting microscope depending on the nature of the character. All spikelet measurements were taken using an ocular micrometer on a dissecting microscope and were obtained from one mature spikelet from each specimen. Panicle measurements were taken using a standard metric ruler. Principal components analysis (PCA) of the standardized data was conducted using Kovach (2005).

RESULTS AND DISCUSSION

An initial PCA of all OTUs indicated morphological differences with 83% of the variability among specimens occurring along the first three components (Table 2). This is due in part to high variable-to-variable correlations among various discrete features of leaf blade pubescence, type of blade involution and curling, thickness of margins, and shape of nodes (Table 3); the high correlations render these features taxonomically important.

Component I accounted for 60.1% of the variability among OTUs, mostly reflecting weak correlations of vegetative features. Component II accounted for 14.9% of the variability, correlating variation in awn and glume lengths, and Component III correlated with pulvini and panicle length (Table 2).

Dispersion of OTUs was greatest along the first two components, with resolution between two morphologic groups occurring along component I (Fig. 2). The two groups were distinguished by a combination of vegetative and spikelet features. OTUs corresponding to Group 1 are characterized by leaf blades folded and straight (Fig. 3), gibbous nodes (Fig. 4), lacking pilose hairs on the adaxial surface, margins not thickened (Fig. 5), smaller glumes, shorter awns, and shorter callus to awn lengths (Figs. 6–7). OTUs clustered in Group 2 are characterized by contrasting features: curling leaf blades (Fig. 8), terete nodes (Fig. 9), leaf blades flat with thickened margins and prominent pilose hairs on the adaxial surface (Fig. 10), larger glumes, longer awns, and longer callus to awn lengths (Figs. 11–12). The type of *Aristida gibbosa* fell within Group 1, and the types of *Aristida sorzogonensis* and *A. orizabensis* fell within Group 2. The placement of the type specimen of *A. marginalis* between Groups 1 and 2 is a result of its having some features of Group 1 (gibbous nodes, branching culms) and some features of Group 2 (flat curling blades, adaxial pubescence).

Because members of Group 2 had previously been identified as three different species (*marginalis*, *orizabensis*, *sorzogonensis*), as well as including both pulvinate and non-pulvinate panicles, a second PCA

TABLE 1. Morphological features scored for principal components analysis, showing discrete and continuous features and how each was scored.

Discrete Features	**Feature Present = 1**	**Feature Absent = 0**
BRANCHING	culms branched	culms unbranched
NODES	nodes terete	nodes gibbous
CURLING	leaf blades curling	leaf blades straight
INVOLUTION	leaf blades flat	leaf blades folded
MARGINS	margins thickened	margins not thickened
PUBESCENCE	adaxial surface pilose	adaxial surface glabrous
PULVINI	panicle pulvinate	panicle non-pulvinate
Continuous Features	Feature Measurement	
PAN	panicle length (cm)	
G1L	glume 1 length (mm)	
G2L	glume 2 length (mm)	
CALAWNL	length from callus to awn (mm)	
CENTAWNL	central awn length (mm)	
LATAWNL	lateral awn length (mm)	

TABLE 2. Factor loadings for the first three components of the principle component analysis of all OTUs. Loadings less that ±0.250 have been replaced by zero.

	Component 1	**Component 2**	**Component 3**
Blade adaxial pubescence	0.335	0	0
Central awn length	0	0.504	0
Blade curling	0.337	0	0
Culms branching	0	0	0
Glume l1 length	0.263	0.291	-0.372
Glume 2 length	0.262	0	-0.39
Blade involution	0.337	0	0
Lateral awn length	0	0.476	0
Callus to awn length	0.309	0	0
Blade margins	0.337	0	0
Node shape	0.335	0	0
Pulvini	0	0	0.416
Panicle length	0	0.351	0.663
Total	60.1%	14.9%	8.0%

was conducted on all 54 OTUs of Group 2 (Fig. 13). The first three components of the PCA explained 82% of the variability of this second analysis (Table 4). Dispersion of OTUs along component I was a function of variability in awn lengths, glume lengths, and callus to awn length. Component II revealed differences in the central awn, glume two, and panicle lengths, as well as the pulvini development. Component III corresponded to variation in panicle length and pulvini development (Table 4).

Dispersion of Group 2 OTUs reveals no further clear morphological distinctions, nor a clear separation between pulvinate and non-pulvinate forms, in spite of these being visually distinctive. Axillary pulvini cause panicle branches and pedicels to spread outward, giving the panicle a somewhat diffuse appearance, contrasting with the dense contracted appearance of non-pulvinate panicles (Figs. 14–17).

In summary, spikelet features are deceptively similar among the three species analyzed, and may lead one to consider them as conspecific. In contrast, vegetative features, though often thought to be of lesser value in grass taxonomy, serve very well in distinguishing the species.

Table 3. Similarity matrix showing variable by variable correlations for PCA of all OTUs.

	PUBESCENCE	CENTAWNL	CURLING	BRANCHING	G1L	G2L	INVOLUTION	LATAWNL	CALAWNL	MARGINS	NODES	PULVINI	PAN
PUBESCENCE	1.000												
CENTAWNL	0.366	1.000											
CURLING	0.977	0.355	1.000										
BRANCHING	-0.654	-0.259	-0.638	1.000									
G1L	0.545	0.577	0.538	-0.373	1.000								
G2L	0.577	0.484	0.565	-0.370	0.909	1.000							
INVOLUTION	0.977	0.355	1.000	-0.638	0.538	0.565	1.000						
LATAWNL	0.381	0.897	0.380	-0.244	0.582	0.510	0.380	1.000					
CALAWNL	0.732	0.548	0.739	-0.574	0.723	0.725	0.739	0.554	1.000				
MARGINS	0.977	0.355	1.000	-0.638	0.538	0.565	1.000	0.380	0.739	1.000			
NODES	0.954	0.342	0.977	-0.676	0.541	0.565	0.977	0.372	0.756	0.977	1.000		
PULVINI	0.589	0.364	0.603	-0.390	0.372	0.283	0.603	0.346	0.435	0.603	0.594	1.000	
PAN	0.100	0.361	0.066	0.118	0.122	0.149	0.066	0.251	0.133	0.066	0.076	0.191	1.000

TAXONOMIC TREATMENT

Consequent to the results of the PCA, three species are recognized (in addition to *A. liebmannii*, which was not analyzed in this study): *Aristida gibbosa* (Group 1 OTUs), *Aristida sorzogonensis* (Group 2 OTUs), and *Aristida marginalis* (represented solely by the type specimen). Variation in features is described in Table 5.

The recognition of *Aristida marginalis* (based on the two isotypes from a single collection) is problematic, since so little is known about it. It is distinguished from the other two species by a suite of peculiar vegetative features: taller, more robust culms with numerous nodes and conspicuously short sheaths, about half as long as the internodes, exposing the many gibbous nodes. Other features are a mix of *A. gibbosa* and *A. sorzogonensis*: flat, curling blades with adaxial pilose hairs characteristic of *A. sorzogonensis*, and gibbous nodes and branching culms characteristic of *A. gibbosa*. We leave the name *A. marginalis* intact until further analyses are possible.

KEY TO THE SPECIES OF THE *ARISTIDA GIBBOSA* COMPLEX

1. Lemma lacking a beak, the awns almost immediately diverging from the not-twisted apex of the lemma body; awns 2–3 cm long ____ **1. A. liebmannii**
1. Lemma with a well developed beak, often twisted prior to the divergence of awns; awns (0.5–)1–2 cm long.
   2. Blades folded or rolled, straight, the margins not thickened, the adaxial surface glabrous ____ **2. A. gibbosa**
   2. Blades flat, curling, the margins thickened, the adaxial surface pilose with long, scattered hairs.
      3. Nodes evidently gibbous, bulging on one side; culms branching above the base, with 7–8 nodes elevated above the base ____ **3. A. marginalis**
      3. Nodes not gibbous, not bulging; culms generally not branching above the base, with 0–4 nodes elevated above the base ____ **4. A. sorzogonensis**

1. Aristida liebmannii E. Fourn., Mexic. pl. 2:78. 1886. TYPE: MEXICO: Veracruz: Mirador, Apr 1842, *F.M. Leibmann 662* (HOLOTYPE: C; ISOTYPES: MO!, US-207485, US-991666 (fragm. ex LE), US-1389797).

We have studied only two specimens: the isotype at MO and an additional specimen (*Burch 6143A*) from Honduras. A brief diagnosis follows [Pohl & Davidse (1994) provide a fuller description]: Sheaths glabrous; blades flat (rolled upon drying or at the ends of the blades), with thickened margins; collar and throat glabrous; panicles narrow, elongate, non-pulvinate, but the lower branches somewhat flexuous and naked at the base; glumes inverse, the first 10–12 mm long, the second 8–9 mm long; lemmas involute, sulcate, a beak absent, the awns diverging immediately at the tip of the lemma; awns 2–3 cm long, ± equal in length.

The combination of a sulcate lemma and long awns is immediately distinctive.

Distribution.—Mexico (Veracruz) and Honduras.

2. Aristida gibbosa (Nees) Kunth, Enum. pl. 1:189. 1833. BASIONYM: *Chaetaria gibbosa* Nees, Agrostologia Brasiliensis, 383. 1829. TYPE: BRAZIL: in camis agrestivus provinciae piauhianae et Minarum generalium, May, *K.F.P. von Martius 14* (HOLOTYPE: M; ISOTYPES: LE-TRIN-1286.01,US-865702 fragm. ex M! & photo!).

Aristida gibbosa is characterized by blades that are folded or rolled, stiffly erect, glabrous, and usually lacking thickened margins. The culms regularly branch above the base and have prominently gibbous nodes, with 2–6(–8) nodes elevated above the base. Panicles are narrow and non-pulvinate.

Distribution.—South America: Bolivia, Venezuela, British Guiana, and Brazil (Fig. 18).

Specimens examined. **BOLIVIA. Santa Cruz:** Santa Cruz, Nuflo de Chavez, Serrania San Lorenzo 10km W of San Javier, 17 Apr 1986, *T. Killeen 1979* (US). **BRAZIL. Without State:** No locality, no date *N. Glaziou 20104, 20106* (US). **Bello Horizonte:** campo, 27 Apr 1936, *M. Barret 4521* (US). **Amazonia:** Estrada macapa-Clevelandia, km 50, 31 Aug 1955, *G.A. Black 18544* (US). **Federal District:** 3km W of the Goias-Distrito Federal border along Highway BR-020-030, 9 Apr 1976, *Davidse et al. 12170* (MO). **Goias:** ca. 15 km (straight line) S of Goias Velho, 10 May 1973, *W.R. Anderson 10039* (MO); no locality, no collector, 20 Apr 1898, *22567* (F); rocky hillside with campo and wooded outcrops, ca. 10 km S of Alto do Pariso, 20 Mar 1969, Irwin et al. 24781 (US); ca. 30 km (straight line) S. of Caiaponia, 29 Apr 1973, *W.R. Anderson 9424* (MO); cerrado on rocky slopes, ca. 38 km N of Veadeiros, 16 Mar 1969, *Irwin et al. 24524* (US). **Maranhao:** "Ilha de Balsas" Region, between the Rios Balsas and Parnaiba, 20 Jun 1962, *Eiten et al. 4865* (US). **Mato Grosso:** in cerrado formation on very sandy soil, 4 Jul 1968, *Ratter et al. 2081* (MO). **Minas Gerais:** Sierra do Cipo, 5 Aug 1936, *W.A. Archer 5028* (US); Lagon Santa, serras a 20 km da cidade, 7 Apr 1951, *G.A. Black 11695* (US); Estado de Minas Gerais, 1 Jan 1951, *Pires et al. 2925* (US); Municipio de Sao Goncalo. BR040, km 251, open cerrado, 25 Jul 1984, *Mori et al. 16988* (MO, US). **Roraima:** along Boa Vista-BV 8 road (BR 174) km 76

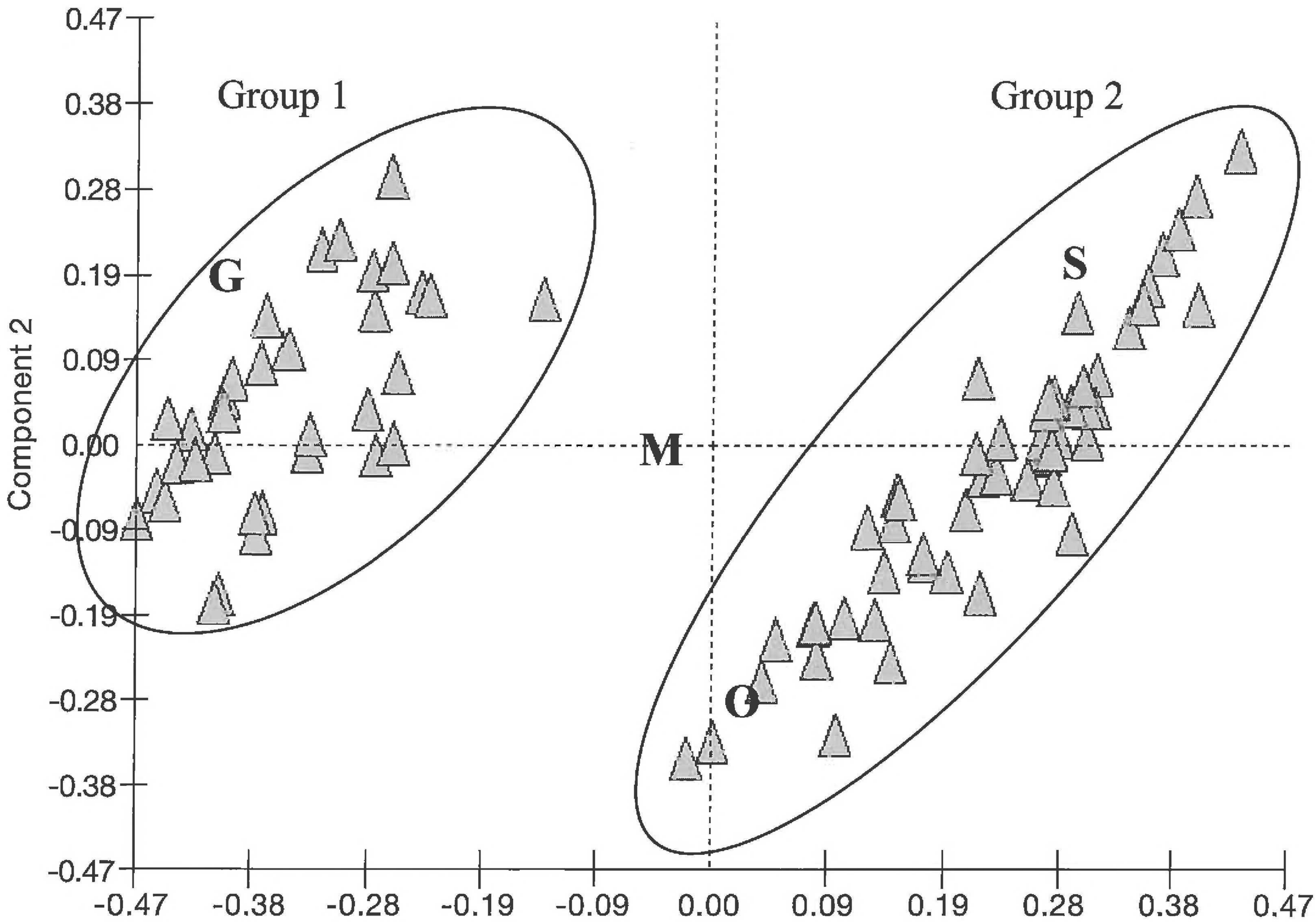


Fig. 2. Dispersion of all OTUs along components I and II of PCA of Aristida gibbosa complex. G = type of *A. gibbosa*. M = type of *A. marginalis*. S = type of *A. sorzogonensis*. O = isosyntype of *A. orizabensis* (*Müller 2103*, US).

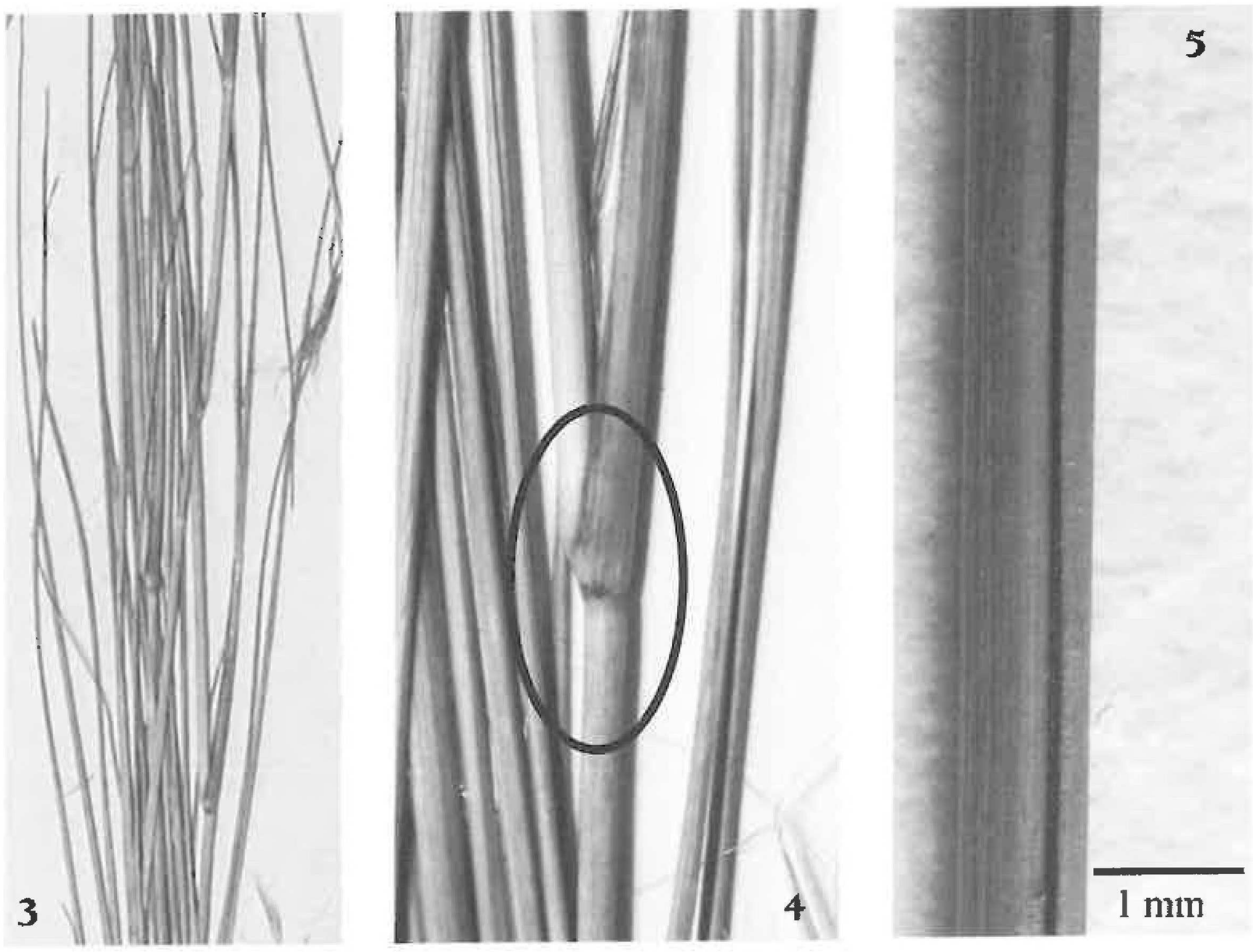
by Uraricoera river, 8 Oct 1977, *Coradin et al. 545* (MO); NE Roraima, ca. 110 km NE of Boa Vista between Bonfim and Guyana border on Tacutu River, 20 Oct 1977, *Coradin et al 792* (US). **BRITISH GUIANA. Rupununi:** no locality 1 Sep 1945, *Fraser, Dr. 378* (US); St. Ignatius dry lateritic ridged savanna 350 ft, 25 Jul 1963, *R. Goodland 22* (US). **VENEZUELA. Anzoategui:** Distrito Bolivar: Rocky mountain savanna, just S of El Zamuro, Fila El Purgatorio, 9 airline km NE of of Bergantin, 24 Nov 1981, *Davidse et al. 19319* (MO). **Aragua:** Carretera Mracay - Choroni, vertiente sur; grama relativemente escasa, en la sabana, 11 Sep 1963, *P. Montaldo 3744* (MO); 12km S of Alto de Choroni (the highest point along the road) on road to Maracay, 14 Nov 1971, *G. Davidse 3068* (MO); 10 km SE of Rancho Grande along road to Maracay, 14 Nov 1971, *Davidse G. 3053* (MO). **Bolivar:** Distrito Piar, middle part of Rio Purpur, affluent of Rio Ambutuir, along trail to Uriman, 30 Nov 1982, *Davidse et 23010* (MO); betweeen Uruyen and Pie de la Roca, SE base of Auyan-tepui, 24 Nov 1982, *Davidse et al. 22559* (MO). **Sucre:** 7 km E of the Mochima Hwy. intersection along Hwy. 9 between Cumana and Puerto La Cruz, 16 Dec 1973, *G. Davidse 5027* (MO).

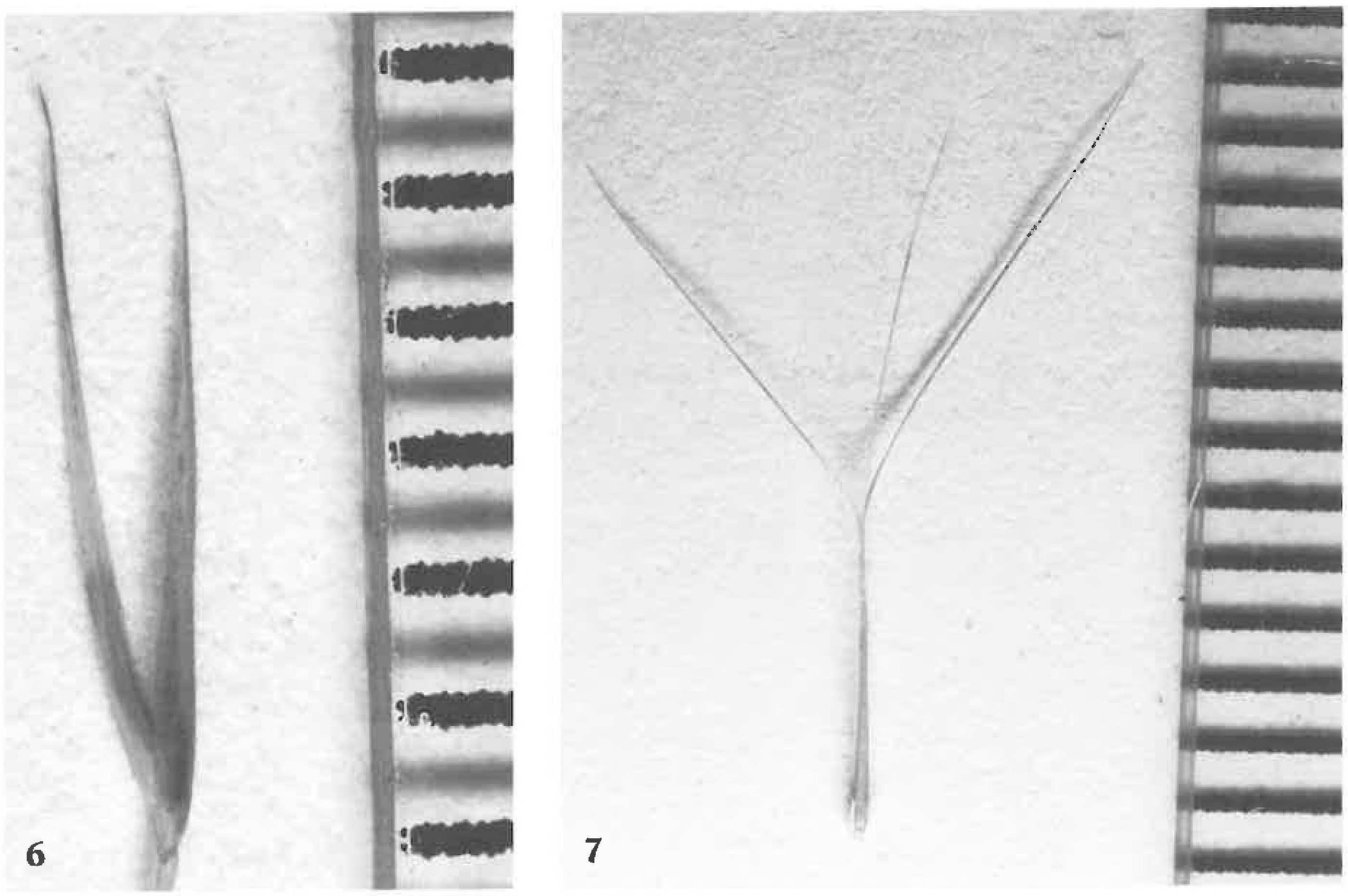
3. Aristida marginalis Ekman, Ark. Bot. 10(17):23, t. 3, f. 2, t. 6, f. 12. 1911. Type: BRAZIL. Matto Grosso: Cuiba, in margine silvulae ('capão') loco sicco, graminoso, arenoso-argilloso, 26 Apr 1903, *G.O. Malme 3143* (holotype S; isotypes G!, US-702283!, US-81202 fragm. ex S!).

Aristida marginalis is known only from the type collection, and is characterized as follows: culms robust, generally about twice as thick as in *A. gibbosa* or *A. sorzogonensis*, branching above the base, with numerous (7–8) nodes elevated above the base; sheaths short, about ½ the length of the internode, straw-colored and contrasting with the pale greenish internode; blades flat, curling, with thickened margins, pilose on the adaxial surface; panicles narrow, but weakly pulvinate.

Distribution.—Known only from Brazil: Matto Grosso, Cuiba (Fig. 18).

The name *Aristida marginalis* has been applied to similar plants from North America, many of which

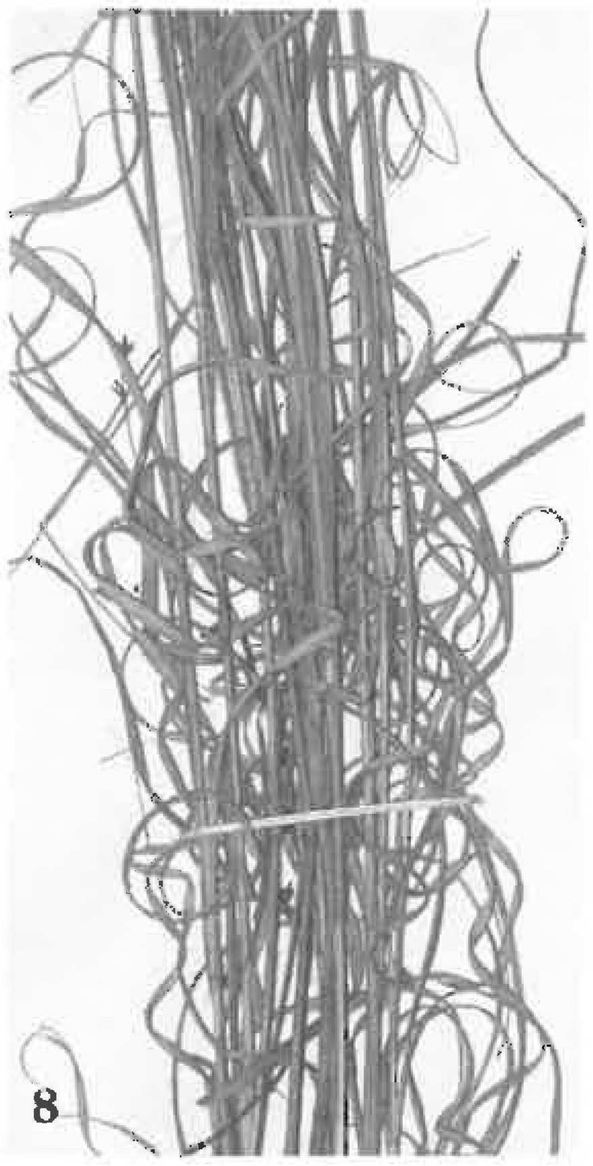




Figs. 3–7. 3. Straight leaf blades of Group 1 OTUs. 4. Gibbous nodes of Group 1 OTUs. 5. Folded leaf blade with thin margins and no adaxial pubescence, characteristic of Group 1 OTUs. 6. Glumes of Group 1 OTUs. 7. Floret of Group 1 OTUs. Scales in mm.

are conspicuously pulvinate, particularly collections reported as such by Howard Scott Gentry (1942) from the Rio Mayo region in western Chihuahua. All of these North American plants fall well within the *A. sorzogonensis* cluster on the PCA, and differ from the true Brazilian *A. marginalis* in the features given in the key.

Further field and herbarium work are needed to fully explain the distribution and variation of *Aristida marginalis*. Its apparent intermediacy between *A. gibbosa* and *A. sorzogonensis* seems coincidental, and not a result of hybridization or introgression. As with many species of *Aristida*, species boundaries are likely to be delicate, yet decipherable, and the name should not be discarded as inconsequential.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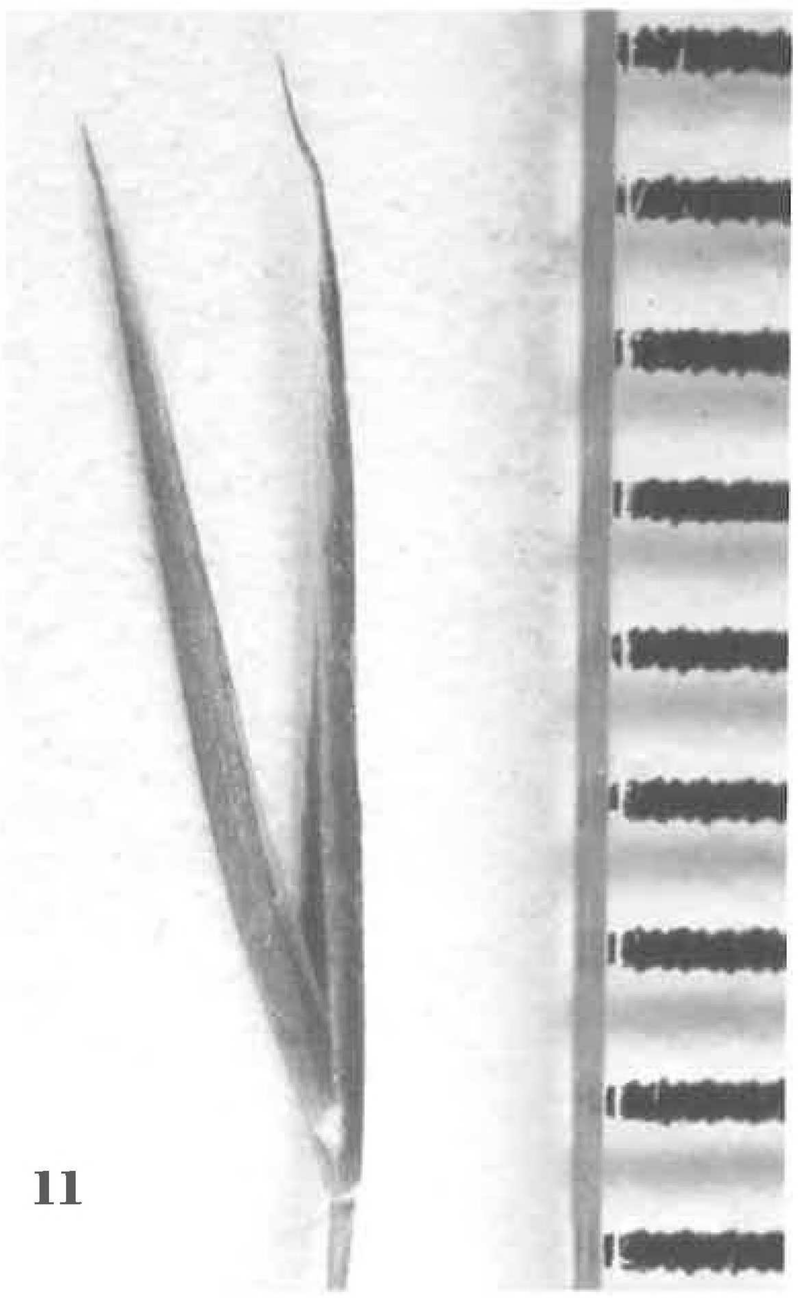
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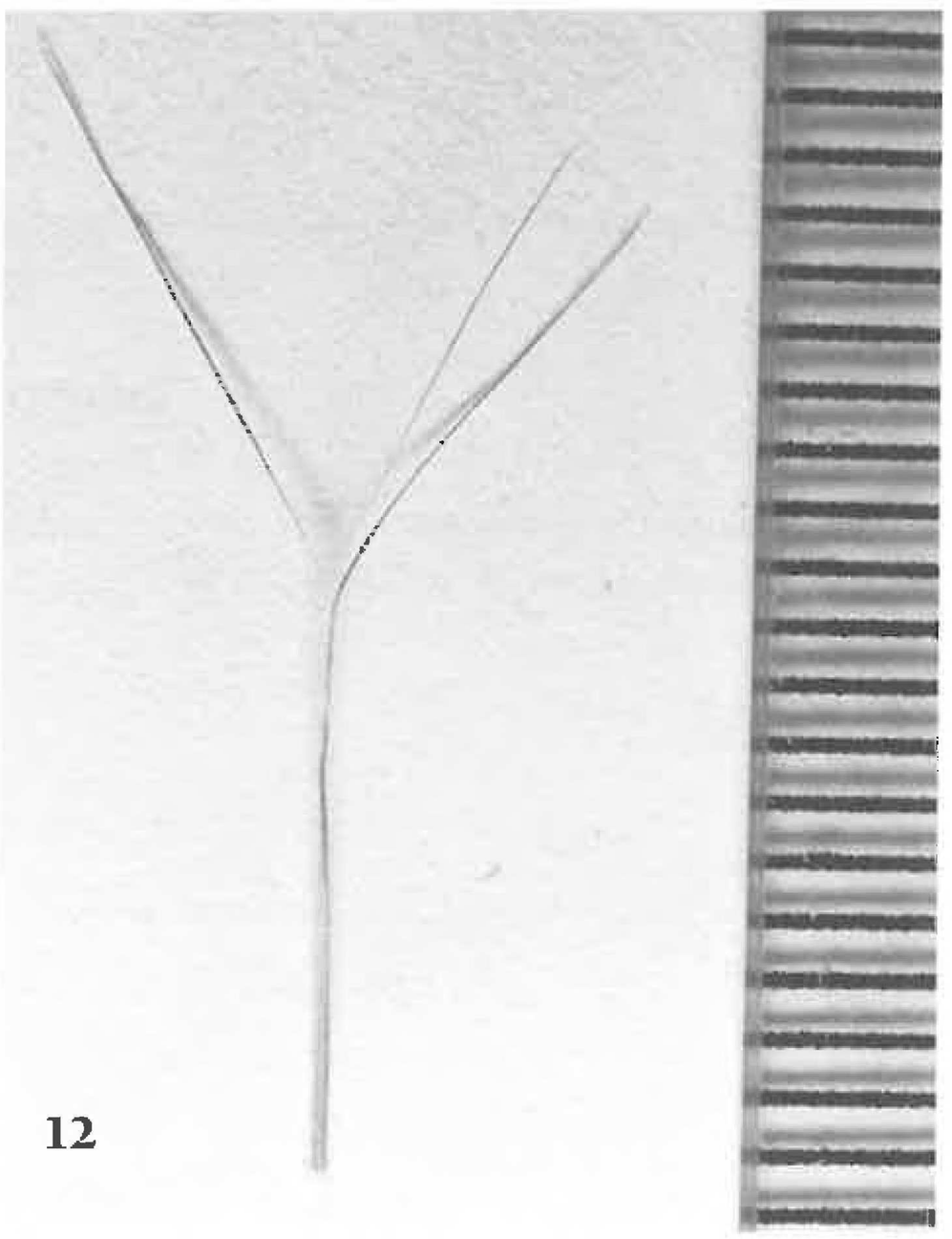
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Figs. 8–12. 8. Curling leaf blades of Group 2 OTUs. 9. Terete nodes. 10. Flat leaf blade with thickened margins and prominent pilose hairs on the adaxial surface, characteristic of Group 2 OTUs. 11. Glumes of Group 2 OTUs. 12. Floret of Group 2 OTUs. Scales in mm.

4. Aristida sorzogonensis J. Presl, in C. Presl, Reliq. haenk. 1(2–4):224. 1830. Type: in Luzonia ad Sorzogon, *T. Haenke s.n.* (holotype: PR photo!; isotypes: LE fragm., PRC photo!, US-81256 fragm. ex W! & photo!, W).

Distribution.—Mostly Mexico and Central America, with a few specimens from northern South America (Fig. 18).

Aristida sorzogonensis is characterized by blades that are flat and curling, with pilose hairs on the adaxial surface and with thickened margins. The culms do not branch above the base and the nodes are not gibbous, with 0–4 nodes elevated above the base. Panicles may be pulvinate or non-pulvinate, which is a minor feature, but the visual differences are immediately noticeable (Figs. 14–17). As has been done

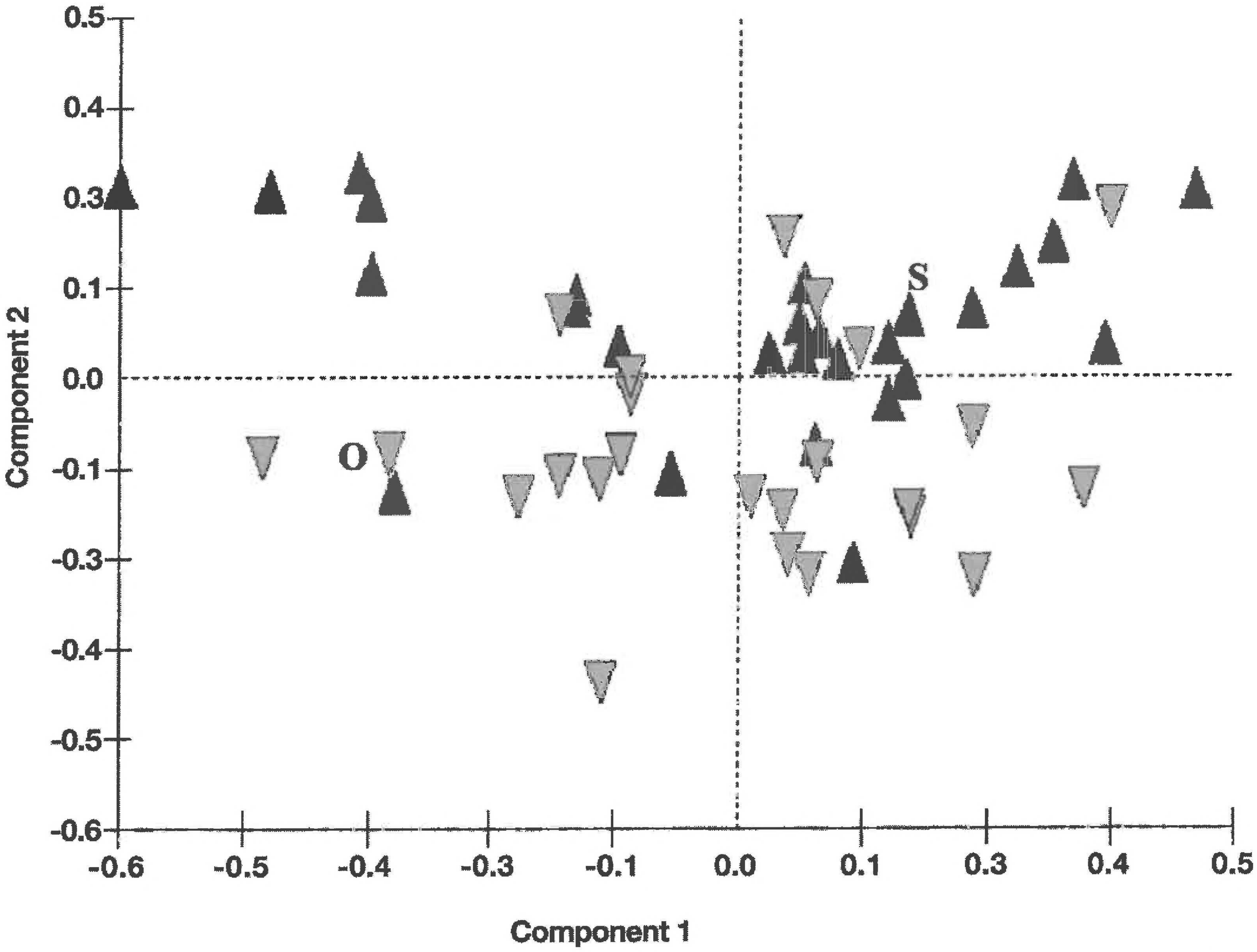
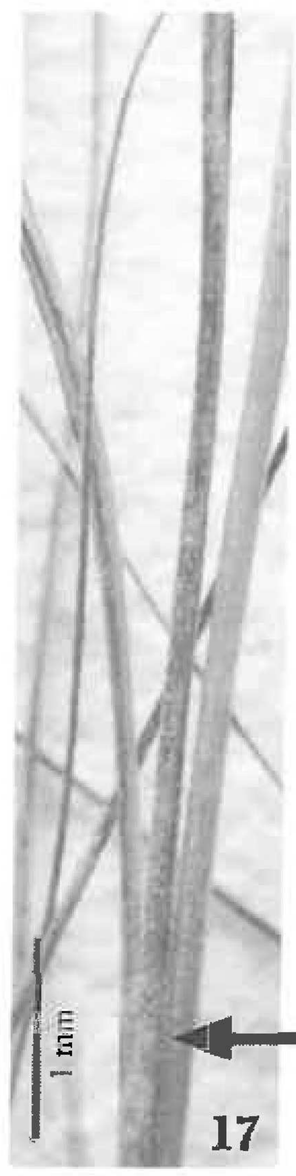


Fig. 13. Dispersion of OTUs along components I and II of PCA of specimens corresponding to the Group 2 cluster: S = type of *A. sorzogonensis*. O = isosyntype of *A. orizabensis* (*Müller 2103*, US). Black triangles = pulvinate form. Gray triangles = non-pulvinate form.

Table 4. Factor loadings for the first three components of the principle component analysis of Group 2 OTUs. Loadings less that ±0.250 have been replaced by zero.

	Component 1	Component 2	Component 3
Blade adaxial pubescence	0	0	0
Central awn length	0.451	0.309	0
Blade curling	0	0	0
Culms branching	0	0	0
Glume 1 length	0.468	0	-0.262
Glume 2 length	0.427	-0.376	0
Blade involution	0	0	0
Lateral awn length	0.466	0	0
Callus to awn length	0.407	0	0
Blade margins	0	0	0
Node shape	0	0	0
Pulvini	0	0.516	-0.815
Panicle length	0	0.615	0.406
Total	48.1%	22.4%	11.5%



FIGS. 14–17. 14. Open panicle with pulvini in the axils of the panicle branches and pedicels. 15. Pulvini in axils of pulvinate panicle (arrow). 16. Contracted panicle lacking pulvini in the axils of the panicle branches. 17. Axils lacking pulvini (arrow).

within *A. purpurea* and *A. pansa* (Allred 1984a; Allred & Valdes-Renya 1997) forma are recognized based on pulvini development:

KEY TO THE FORMS OF *ARISTIDA SORZGONENSIS*

Panicles pulvinate, with pulvini in the axils of branches, branchlets and pedicels, the panicle at least slightly open and somewhat diffuse_____ **4a**. f. ***sorzogonensis***

Panicles non-pulvinate, rarely developing pulvini in the axils of branches, branchlets or pedicels, the panicle consistently narrow and contracted _____ **4b**. f. ***orizabensis***

Table 5. Comparison of features of *Aristida gibbosa, A. sorzogonensis,* and *A. marginalis*.

	A. gibbosa		A. sorzogonensis				A. marginalis
		non-pulvinate			pulvinate		type specimen
Continuous Characters	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Range
Panicle length (cm)	17.6 ± 5.4	9.0–31	16.0 ± 4.9	6.5–25.0	19.7 ± 3.9	9.0–27.5	16.0–18.0
Glume 1 length (mm)	6.9 ± 1.1	4.9–10.3	9.0 ± 1.4	6.2–11.0	8.4 ± 1.6	4.8–10.7	7.2–8.0
Glume 2 length (mm)	6.2 ± 1.0	5.0–9.1	8.1 ± 1.3	6.0–10.5	7.4 ± 1.3	4.5–9.1	6.6–7.3
Callus to awn length (mm)	6.4 ± 1.4	4.8–11.0	9.7 ± 1.5	5.7–12.0	9.5 ± 1.7	5.7–13.0	6.2–7.3
Central awn length (mm)	11.1 ± 2.0	8.3–18.0	12.7 ± 2.4	8.4–17.5	12.8 ± 2.3	8.3–18.1	13.3–15.4
Lateral awn length (mm)	8.4 ± 1.7	6.0–14.0	10.2 ± 1.7	6.0–14.0	10.2 ± 2.5	5.5–15.8	9.5–12.1
Discrete Characters							
Culms	branched	unbranched	unbranched	branched			
Nodes	gibbous	terete	terete	gibbous			
Blades	stiff & erect	lax & curling	lax & curling	lax & curling			
involution	folded	flat	flat	flat			
margins	not thickened	thickened	thickened	thickened			
adaxial pubescence	glabrous	prominently pilose	prominently pilose	pilose			
Panicle	non-pulvinate	non-pulvinate	pulvinate	weakly pulvinate			

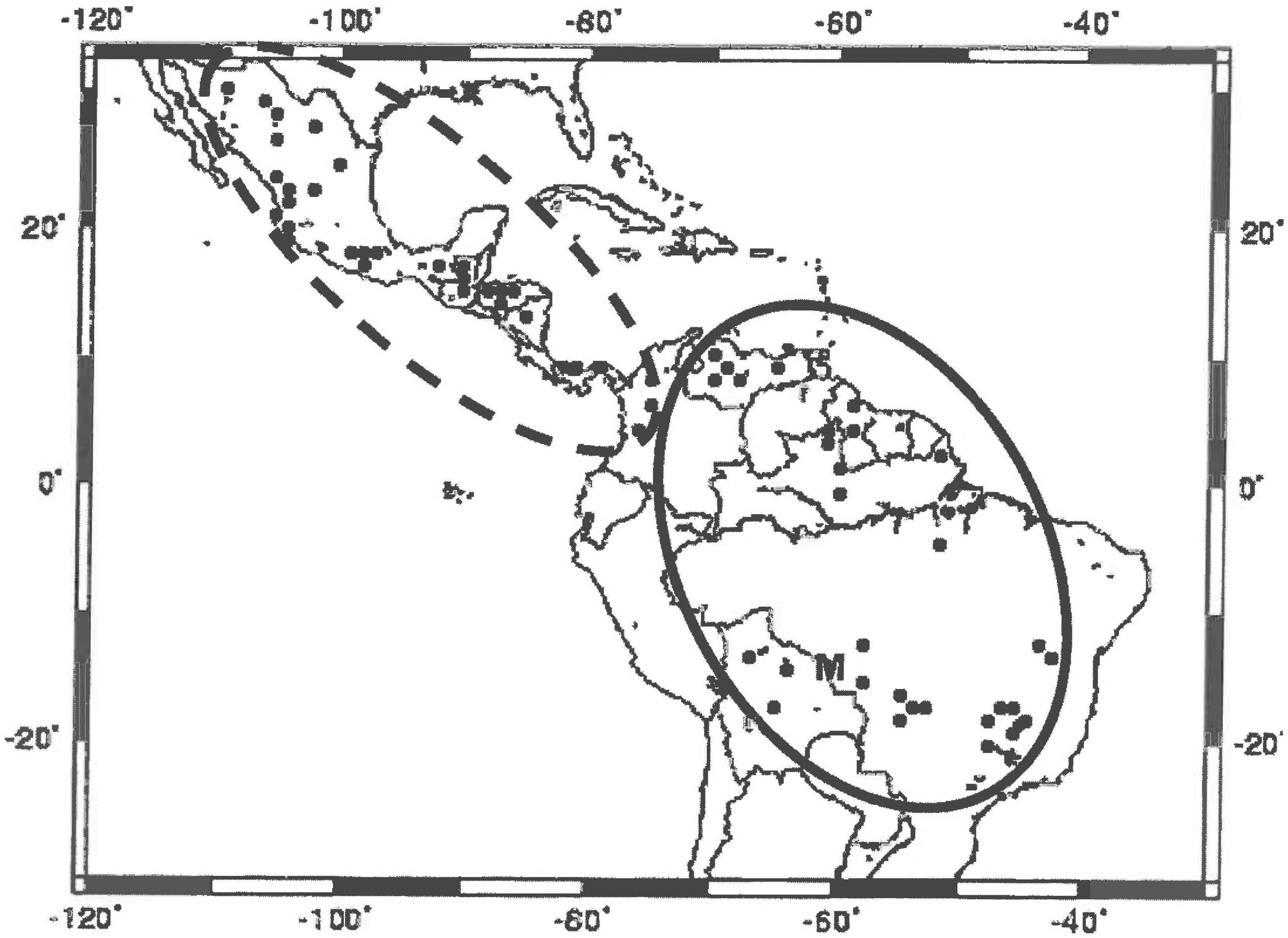


FIG. 18. Distribution map of species in the *Aristida gibbosa* complex. Circles indicate collection locations of herbarium specimens used in the study. Some dots represent more than one collection. Dashed line = *A. sorzogonensis*. Solid line = *A. gibbosa*, M = Type specimen of *A. marginalis*.

4a. *Aristida sorzogonensis* f. *sorzogonensis*

Distribution.—Mostly Mexico (Chiapas, Chihuahua, Jalisco, Michoacan, Nayarit, Sinaloa, Tepic) and Central America (Costa Rica, Honduras, Panama), with a few specimens from Columbia and Bolivia.

Specimens examined. **COLOMBIA. Santa Marta:** no locality, *H.H. Smith 136* (US). **BOLIVIA:** between Aguas Zembrades and Pinal,trail to Cerro SanLucas Bolivar, 1400 ft, 12 Aug 1944, *Drew, W.B. 146* (US). **COSTA RICA. Puntarenas:** 3 km N of the Carretera Interamericana along the road to Boruca, 12 Dec 1968, *Pohl et al. 11602* (F). **HONDURAS. El Paraiso:** Wuebrada del Muro, road to Yuscaran, open ground, 5 Nov 1951, *J.R. Swallen 11327* (MO). **Morazan:** Sabanas abiertas a lo largo de la carretena, Las Mesas, 23 Nov 1948, *A. Molina 1707* (US); rocky pine woods, hills around Zamorano valley, 2 Nov 1951, *Swallen J.R. 11259* (US); rocky pine-oak slopes, 15 Oct 1951, *J.R. Swallen 10751* (US); rocky pine woods, hills around Zamorano valley, 2 Nov 1951, *J.R. Swallen 11256* (US); colinas y bosque micto entre Las Mesas y Guayabillas 5km empalme carretera dalini yuscaran, 04 Nov 1963, *A. Molina 13164* (F). **MEXICO. Chiapas:** Municipio Chicocucelo, Belen, 1 km E of Las Sabanas, 2 km SE of Chicomucelo, 18 Nov 1984, *Davidse et al. 30037* (MO). **Chihuahua:** Rio Mayo; Upper sonoran; oak flat, Guasaremos, 26 Sep 1935, *H.S. Gentry 1873* (ARIZ, MO, NMCR, WIS, US). **Jalisco:** 20 km Guadalajara-Tepic, 26 Sep 1946, *Hernandez et al. 2745* (US); arroyo sin nombre (pero con agua corriente) 3.2 km al W de Las Marias; 15 km por camino al E de Cuautitlan en el camino a Avotitlan, 08 Jan 1985, *T.S. Cochrane 10987* (WIS). **Michoacan:** along road from Tsitzio-Tiquicheo-Huetamo-Altamirano, 7 Oct 1953, *E.R. Sohns 906* (US). **Nayarit:** 10 km al E de Tepic por la carretera a Mazatlan, 18 Nov 1983, *F.J. Santana 1426* (MO); 13 km NW of TEPIC (Municipio de Tepic) along highway 15, 18 Nov 1983, *Solheim et al. 971* (WIS); steep treeless hills 10 mi SE of Tepic, 6 Oct 1952, *Mcvaugh R 13384* (US). Sinaloa: Cerro Colorado, 1 Nov 1904, *Brandequa* (US); Mesa Malqueson, Cerro Colorado; open rocky slopes on oak savannah, 2500 ft, 8 Dec 1939, *H.S. Gentry 5179* (MO). **Sonora:** Sierra Tecurahui, SE Sonora, 4250 m, 27 Oct 1961, *Gentry et al. 19380* (US). **Tepic:** no locality, 6 Feb 1892, *Dr. E. Palmer 1916* (US). **PANAMA:** between Paso Del Arado and Ola, province of Cocle, in savannas and thickets, 7 Dec 1911, *H. Pittier 5019* (US); vicinity of Ola, province of Cocle, 7 Dec 1911, *H. Pittier 5047* (US); Picacho de Ola, province of Cocle, 8 Dec 1911, *H. Pittier 5066* (US); ca. 10 km SW of San Carlos along the Inter-American Hwy, 18 Nov 1975, *Davidse et al. 10128* (MO).

4b. Aristida sorzogonensis f. **orizabensis** (E. Fourn.) Strahan & Allred, comb. nov. Basionym: *Aristida orizabensis* E. Fourn., Mexicanas Plantas II:78. 1886. Type: MEXICO. Veracruz: Valle de Orizaba, *J.H. Schaffner 136* (syntypes: P; isosyntypes LE); MEXICO: *F. Müller 2103* (syntype: P; isosyntypes: L, NY! US!). The name *Aristida orizabensis* E. Fourn. remains to be lectotypified, being based on two collections (*Schaffner 136* and *Müller 2103*) cited by Fournier (1886). The specimens at P and LE were unavailable. Our concept of *Aristida orizabensis* Fournier is based on isosyntypes of *Müller 2103* at NY and US.

Distribution.—Mostly Central America (Guatemala, Honduras, Panama), with fewer specimens from Mexico (Sinaloa, Guerrero) and Columbia.

Specimens examined. **COLOMBIA. Huila:** 3 km SE of Neiva, Huila, 1700 m, 23 Feb 1945, *Little et al. 9470* (US); 6 km SE of Altamira along road to Florencia, 9 Jan 1974, *G. Davidse 5602* (MO). **GUATEMALA. Jalapa:** dry rocky pine-clad between Monjos and Jalapa, ca. 10 mi S Jalapas, 29 Nov 1939, *J. Steyermark 32176* (F). **Without State:** in wet ground in margin of oat field between Guatemal city and Jutiapa, 10 Oct 1944, *Goodman et al. 3696* (F). **HONDURAS. El paraiso:** road to Yuscaran open places, about km 2, 5 Nov 1951, *J.R Swallen 11351* (US); rocky slope, in pine woods, beyond Rio San Francisco, 1 Nov 1951, *J.R. Swallen 11212* (US). **Morazan:** 20 km N of Talanga along the road to Cedros Pinus-Quercus forest on hills, 4 Oct 1986, *Davidse et al. 31584* (MO); Santa Ines, 4 Nov 1943, *J.V. Rodriguez 1486* (F); open grassy hills, 7 Nov 1951, *J.R. Swallen 11386* (US); Santa Inez, 5 km E of El Zamarano, 19 Dec 1978, *Pohl et al. 13738* (MO); Colinas y bosque mixto entre Las Mesas y Guayabillas, 5 km empalme carretera dalini yuscaran, 04 Nov 1963, *A.Molina 13167* (F). **Without State:** in mixed oak-pine forest near Piedra Herrada, 11 Sep 1949, *L.O. Williams 15975* (F); in pine woods, near Jicarito, 5 Dec 1948, *Williamson et al. 14802* (US). **MEXICO. Guerrero:** Ixtapan de la Sal, 12 Oct 1952, *Matuda et al. 27056* (US). **Sinaloa:** between Mazatlan and Durango, 6 Jan 1975, *Beetle et al. 3695* (WIS). **PANAMA. Herrera:** 10 mi S Ocu roadside, 21 Jan 1966, *Tyson et al. 2866* (MO).

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